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FURTHER ARCHAEOLOGICAL EVIDENCE ON THE EFFECTS OF TEOSINTE INTROGRESSION IN THE EVOLUTION OF MODERN MAIZE

BY

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ANOTHER large and significant collection of prehistoric maize cobs (*Zea Mays* L.) with Tripsacoid characteristics that are indicative of introgression from either *Tripsacum* spp. or its maize derivative, teosinte[2] (*Zea mexicana* Reeves and Mangelsdorf), has been provided by the archaeologist, who is the junior author, for botanical analysis. Although there have been about a dozen other collections of prehistoric Tripsacoid cobs from northwestern Mexico and southwestern United States, the present material, which comes from Cebollita Cave in New Mexico, is the first large (2575 cobs), stratified (five levels) collection to become available for statistical treatment.

Our previous statistical study (Galinat, *et al.*, 1956) of Tripsacoid cobs involved a large non-stratified collection from two caves in Arizona. At that time we established

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[2] For the purposes of discussion and consistency, we shall assume, as we have previously, that the immediate source of the introgression represented by these archaeological specimens is from teosinte rather than from less likely hybridization with *Tripsacum*.

the reliability of scoring for teosinte introgression according to the degree of induration by showing that the more indurated archaeological cobs are like modern maize-teosinte derivatives in having a higher specific gravity which is also positively correlated, in modern maize, to number of teosinte chromosomes.

According to this system, induration is subjectively estimated with an arbitrary key of five grades. At grade-1 the glumes and rachis are non-indurated and somewhat flexible. At grade-5 the glumes and rachis are not only highly indurated, but the glumes are curved upwards and at least some pistillate spikelets are borne singly, features which are common in maize-teosinte hybrids, but absent in typical maize.

By applying this method to estimate teosinte introgression in the present stratified material, we may now determine the evolutionary effects of such introgression upon the maize from this site.

Description of the Site

The archaeological maize upon which this study is based was excavated from Cebollita Cave in the Cebolleta Mesa[1] area in Valencia County, New Mexico, about twenty miles south of the town of Grants. The area is bounded on the west by the McCarthys' Lava Flow and on the east by the western slope of Cebolleta Mesa. It is in the Upper Sonoran climatic zone at an elevation of about 7000 feet. The terrain consists of broad valley floors and sheer sandstone cliffs. The cave is located in a vertical sandstone cliff in the Zuni sandstone member. It faces south and opens out on a broad valley, which,

[1] According to the principal maps of the area, the name of the mesa is spelled Cebolleta while the name of the cave which contained the archaeological maize is spelled Cebollita. The latter spelling comes from the Spanish word meaning "little onion."

before channel cutting had commenced, must have been an ideal flood-farming area.

The flora includes piñon pine, juniper, manzanita (*Arctostaphyllos pungens*), sage, blue gramma grass, yucca, bee weed (*Cleome serrulata* Pursh), and several varieties of cacti. Canyon floors in the area normally have a good stand of blue gramma grass mixed with some cacti, yucca, sage brush, and manzanita. Minor depressions are covered by a thick stand of bee plants and sunflowers after the beginning of the rainy season. Scattered stands of juniper and piñon pine are found on the valley floors. Deer, coyotes, prairie dogs, rabbits, lizards, and snakes constitute most of the faunal assemblage.

The climate is semi-arid and precipitation averages about eleven inches annually. The growing season can only be estimated from reports of government stations near Cebolleta Mesa and is thought to be about 110 days long. It is assumed that the climate at the time the cave was inhabited was approximately the same as today.

The site is a fourteen room pueblo situated in Ceboll-ita Cave. The pueblo was built piece-meal and abandoned at least once during its existence. The abundant rock fall from the roof attests to the hazards of life in the cave. An enormous block of sandstone fell from the roof at one time and caused a temporary abandonment of the pueblo. When the pueblo was reinhabited, it was by a group who had a slightly different culture than the previous occupants. Although the cave was inhabited in the Pre-pueblo and Pueblo I periods, the pueblo itself was not constructed until the end of the Pueblo II period. The entire occupation of the pueblo was encompassed within the Early Pueblo III period, from about 1050 to 1200 A.D. as dated by ceramic typology.

Preservation of organic material in the pueblo was variable due to run-off water from the mesa top which flowed

into some of the rooms. Those rooms which remained dry contained large amounts of vegetal remains such as corn, squash, and other seeds, together with cordage, matting, sandals, basketry, and wooden objects. Most of the corn utilized in the present study was found in Rooms B, C, and D in the back of the cave. Room B contained four feet of deposit, the deepest fill in the pueblo.

The archaeological value of the maize under discussion lies in the fact that the excellent stratigraphic evidence indicates an interesting history of human occupation in the pueblo. Room B supplied most of the evidence and most of the maize. Level 5 in Room B marks the earliest occupation of the pueblo. Three hard-packed adobe floors were superimposed at the base of this level. The original maize at the site was found on the uppermost floor and occurred in fifteen concentrations of charred, shelled kernels, ashes, and heat-warped pot sherds. More than 500 charred ears were also found lying on the floor. The concentrations of shelled kernels had been stored in pots and the loose ears must have been hung from the roof beams.

All of the material found in Level 5 and the lower half of Level 4 was burned. A three-foot thick concentration of spalled sandstone slabs was found above Level 5 and the lower half of Level 4. The slabs had spalled off the cave ceiling as a result of the fire that destroyed Room B. In addition, a huge block of sandstone weighing many tons fell across Rooms D and E. The fire and rock fall terminated occupation of the site for a time, but, pending study of the dendrochronological specimens, the duration of the abandonment is unknown.

The Ceramic Assemblage

Reoccupation of the pueblo was accomplished by a group of Indians using a slightly later variant of the Early Pueblo III ceramic types (normal Tularosa phase)

than their predecessors. Greater changes in the type of pottery than those observed would be expected if the period of abandonment had been long. A quarter of the total number of sherds from one room occupied by the newcomers was of the brown paste type, an atypical proportion for the area at that time, but the other rooms do not show as high a proportion.

Perishable Material other than Maize

A large amount of perishable material other than maize was found in the upper levels, including nine sandals, five wooden arrow foreshafts, a number of fragments of basketry and matting and several hundred pieces of plain, fur, or feather-wrapped cordage. One of the sandals is a modified fish-tail type of the kind found throughout the Mogollon area (Cosgrove, 1947, fig. 92-9b; Haury, 1934, plate 41; Bluhm, 1952, p. 271). It is interesting to note in this connection that Cosgrove also found Tripsacoid maize together with this type of sandal in the Hueco Mountain caves. Two of the other sandals were typical of the Four Corners Region in Basketmaker and Pueblo III horizons (Kidder and Guernsey, 1919). A similar type was also found at Bat Cave (Herbert Dick, unpub.) and in Tularosa Cave (Bluhm, 1952, p. 279).

The sandals might suggest that the newcomers originated from somewhere in the Mogollon region, but such a conclusion is based on slim evidence at best. Recent researches in the Cebolleta Mesa area have resulted in the conclusion that there is a region of cultural blending between the Anasazi and Mogollon regions. In this case, since the Cebolleta Mesa area is on the southern periphery of the Anasazi region, it might have received influences from the blend region just to its south. Therefore, it seems likely that the possessors of the Tripsacoid maize may have come from this blend region.

Level 5 Maize

The maize ears from the lowest stratum (Level 5), resemble those of the race "Chapalote," an ancient indigenous race of Mexico described by Wellhausen *et al.*, 1952, and the principal, if not the only race of the early cultures from this part of North America (Mangelsdorf and Lister, 1956). At Bat Cave, New Mexico, a primitive form of Chapalote remaining from an incipient cultivation tradition dates back to between 3500 and 2500 B.C. (Mangelsdorf, 1954). Some of the prehistoric maize from coastal Peru (about 600 B.C.) may also have affinities with Chapalote (Grobman and Mangelsdorf, 1959).

Identification of the original Cebollita maize as Chapalote was possible because most of the ears were perfectly preserved by a carbonization process resulting from incomplete combustion. The original Cebollita maize and Chapalote share the following characteristics. Their ears are cigar shaped, with a slight tapering at both base and tip. Prominent glumes may protrude between the kernels. Small, hard kernels are rounded on top and nearly isodiametric in length, width, and thickness. The vertical rows of these kernels, especially those of 10- and 14-rowed ears, have a strong tendency to twist. A relatively high row number in combination with a slender rachis, forces the cupule wings and paired kernels to interlock[1] slightly with the lateral rows on either side. The interlocking of cupule wings creates the illusion of broad cupules. The actual cupule width (5.5 mm.) is like the kernel width (6.0 mm.) in being only about one-half that of other North American races such as the 8-rowed flour and flint types.

A comparison of the actual values in Cebollita maize

[1] Interlocking of adjacent pairs of kernels, sometimes called tesselation, is also found in a primitive Peruvian race, Confite Morocho, and certain of its derivatives (Grobman, unpub.).

with those of modern Chapalote from the Mexican states of Sonora and Sinaloa and with those of certain early Basket Maker ears (about 800 A.D.) obtained from the studies of Hurst and Anderson (1949) on maize from Cottonwood Cave, Colorado, reveals that the ears from Cebollita Cave are slightly smaller (Table I). The date of the Cebollita maize (about 1050 A.D.) seems to exclude it as a more primitive or inherently smaller type of Chapalote. Rather, reduction may be a depauperate condition resulting from poor growing conditions. The latter suggestion is supported by the fact that the best Level 5 ears compare favorably to those of modern Chapalote and Cottonwood Cave maize.

The termination of Level 5 was marked by a fire which either carbonized or charred all of the original Chapalote cobs and caused a large rock fall from the ceiling, as well as a temporary abandonment of the cave.

Level 4 Maize

Upon reoccupation of the cave, as designated by Level 4, 85% of the cobs changed abruptly to the Tripsacoid type of maize which was becoming widespread throughout southwestern United States during this period (1000–1200 A.D.). Three percent of these were almost exact counterparts of modern F_1 hybrids or hybrid segregates from experimental crosses between maize and teosinte in being two-ranked for at least part of their length, and in having highly indurated, upward-curved glumes (Plate XXIII, cobs C, D). Such highly Tripsacoid cobs were scored as grade-5 according to our system of estimating the degree of teosinte introgression with an arbitrary key of five grades. On the average, the Level 4 specimens were the most Tripsacoid from the entire site, having an average introgression grade of 2.6.

At the other extreme, fifteen percent of the Level 4

EXPLANATION OF THE ILLUSTRATION

PLATE XXIII. A series of cobs from the various levels in Cebollita Cave. The original Chapalote maize (cob A) of Level 5 has some non-carbonized counterparts (cob B) in Level 4. Note the soft glumes of cob B. Level 4 also contains many small highly Tripsacoid cobs (C, D) similar to segregates of experimental hybrids between maize and teosinte. Although Level 3 (cobs E, F, G) marks the beginning of a progressive decrease in the indurative effects of the teosinte introgression, the variability which it had introduced continues to increase. Finally in Levels 2 and 1, there is almost complete recovery from the detrimental effects of the introgression and many of the cobs (H, I) are larger and probably more productive than the original Chapalote maize. About one half natural size.

Plate XXIII

cobs were scored as grade-1, because they had long soft glumes which were structurally similar to the carbonized ones from the original Chapalote in the previous level. Some of the soft-glumed cobs were also identical in all other characteristics to the original specimens except in being non-carbonized. Therefore, the continuity of the population of cobs was not completely broken by the change to Tripsacoid maize.

The sudden change to these Tripsacoid cobs of Level 4 does not preclude a change in maize background from that of the original Chapalote. Teosinte introgression had already occurred much earlier in the Chapalote from other parts of New Mexico (Bat Cave in Catron County, Mangelsdorf and Smith, 1949); it was well established in this race in northwestern Mexico by 750±250 A.D. (Mangelsdorf and Lister, 1956). Inasmuch as Tripsacoid Chapalote was prevalent then and there is no evidence in type of ceramics or sandals of trade from far outside the area, the new variation is attributed to teosinte introgression in Chapalote.

The onset of teosinte introgression caused a marked drop in the average size of cob to the lowest values for the site. The average kernel row-number dropped by 11%, the cob diameter by 10%, and the cob length by 22% below that of the original Chapalote. These reductions represent modification toward the spike of teosinte and are correlated to estimated teosinte introgression in the population as a whole (Plate XXIV, figs. 1, 2, 3).

These reductions in average cob size in the Tripsacoid maize may not reflect a corresponding loss in over-all yield per plant or per acre of plants. Some modern maize breeders have found that a reduction in ear size in teosinte derivatives of maize tends to be compensated for by an increase in number of ears per plant. However, some of the energy in Tripsacoid maize may be diverted away

Plate XXIV

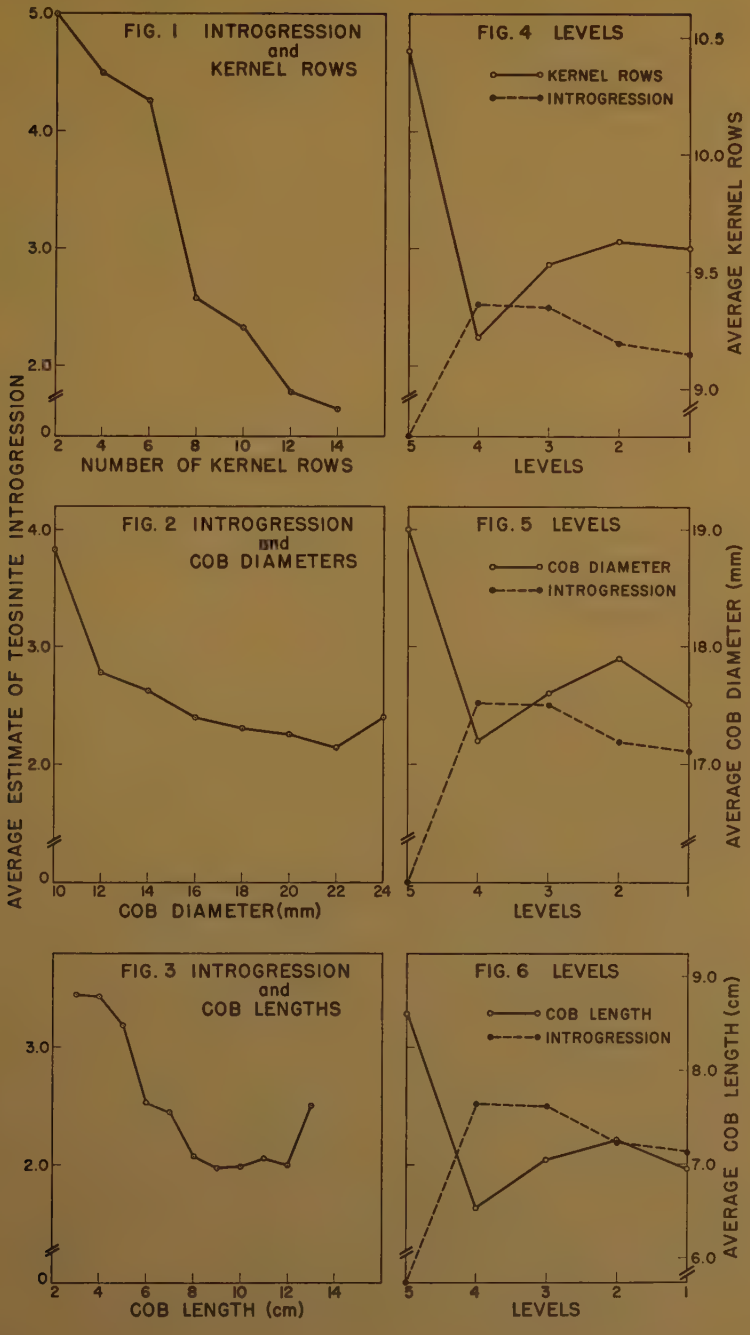
FIG. 1 INTROGRESSION and KERNEL ROWS
NUMBER OF KERNEL ROWS
AVERAGE ESTIMATE OF TEOSINITE INTROGRESSION
FIG. 4 LEVELS
KERNEL ROWS
INTROGRESSION
AVERAGE KERNEL ROWS
LEVELS
FIG. 2 INTROGRESSION and COB DIAMETERS
COB DIAMETER(mm)
FIG. 5 LEVELS
COB DIAMETER
INTROGRESSION
AVERAGE COB DIAMETER (mm)
LEVELS
FIG. 3 INTROGRESSION and COB LENGTHS
COB LENGTH (cm)
FIG. 6 LEVELS
COB LENGTH
INTROGRESSION
AVERAGE COB LENGTH (cm)
LEVELS

from grain production and into the production of strong lignification of the cob and stalk tissues. But even so, such an expenditure on development of a stiff stalk may be necessary to keep the ears erect and away from certain vermin.

The effect of teosinte introgression on cob length is not always detrimental. The longest, as well as the shortest, intact cobs were the most Tripsacoid (fig. 3). Those of intermediate length tended to resemble the original maize in having soft glumes.

The same type of parabolic curvilinear correlation between teosinte introgression and cob-length was also found with the cobs from Richards Cave in Arizona (Galinat *et al.*, 1956). In this previous study the parabolic curvilinear correlation, based on 433 intact cobs, had a value of 0.859, which was highly significant. The nature of the curve was explained by assuming that the long Tripsacoid cobs are the vigorous products of heterozygous teosinte germplasm, while their short counterparts are the detrimental effects of homozygous teosinte germplasm. This explanation may be applied equally well to the cobs from Cebollita Cave. The repetition of the so-called "maize-teosinte heterosis" at another site, indicates that this apparent counterpart of modern hybrid maize may have become widespread at the time just prior to 1200 A.D. in the Southwest. The blending of teosinte germplasm into maize would continue if its presence provided any selective advantage such as that resulting from maize-teosinte heterosis. Under such conditions, the distribution of Tripsacoid maize might become many generations and hundreds of miles removed from teosinte itself.

Level 3 Maize

Level 3 marks the start of a progressive reduction in teosinte contamination or at least a modification of its

expression. In either case, as the indurative effects of this introgression[1] declined, the average cob size retrogressed somewhat toward that of the original pure Chapalote. The reduction in "introgression" was slow at first, being only 8% at this stratum (Level 3) and not in proportion to the far greater recovery in kernel row number, cob diameter, and cob length of 18%, 22%, and 21% respectively (Plate XXIV, figs. 4, 5, 6).

But even as the direct effects of teosinte introgression were apparently diminishing, the variability in cob size which was introduced by this introgression in the previous Level (4), continued to increase in higher levels. For cob diameter, the standard deviations which measure degree of variability, for Levels 5 through 1, were 1.48 mm., 2.12 mm., 2.56 mm., 2.54 mm., and 2.10 mm., respectively. Increases in diameter variance are significant up to Level 3. But for cob length, the expanding variation proceeds one level higher, as shown by the standard deviations for Levels 5 to 1, respectively, as follows: 1.01 cm., 1.89 cm., 2.27 cm., 2.39 cm., and 1.86 cm.

There are several possibilities which may, as a whole or in part, account for the continued increase in variability after a reduction in teosinte introgression. If there was some variability injected by a new non-Tripsacoid race from elsewhere, its effect must have been insignificant because the continuity of the population was not disrupted by a complete break from the features of Chapalote. In addition to an actual reduction in teosinte germplasm, the accumulating variability may have brought about some modification of its indurative effects. Mangelsdorf (1958) suggested, on the basis of experimental

[1] In order to facilitate further discussion, we shall assume that our estimate of teosinte introgression, according to the degree of induration, represents a relative measure of its intensity.

evidence from modern maize-teosinte derivatives, that much of the variation in modern maize is the product not only of recombination of genes from the two species, but also from the mutagenic effects of teosinte germplasm in maize. Similarly, some of the increased variation in the Cebollita maize may be the result of a mutagenic effect of teosinte germplasm.

Level 2 Maize

Proceeding to the next Level (2), the same trends continue: teosinte introgression decreases while average ear-size increases. The extremes in cob-length and cob-diameter held about the same as those of the previous level (Table II). But in the case of cob-length, the various categories became more equally represented with the result that the standard deviation or variability increased. As mentioned previously, the longest cobs are apparently a product of maize-teosinte heterosis. The fact that cob length did not decline with the apparent reduction in introgression at these higher levels might be explained in terms of a selective elimination of deleterious factors from teosinte and/or a buffering against the effects of such factors while beneficial factors involved in maize-teosinte heterosis were retained and blended into the evolving population.

Level 1 Maize

The cobs from the uppermost level represent the final evolutionary product from this site. Although the actual quantity of cobs was less than ten per cent of that from any previous level, it yields some of the longest and best specimens. These superior ears represent a combination of butt fasciation descended from the original Chapalote together with the more lignified and heterotic products of teosinte introgression. Some of these specimens re-

semble the present day maize from the Southwest (Plate XXIII, cob I).

Summary

1. The method of scoring for teosinte introgression according to the degree of induration has been used to study the archaeological record of the role of such introgression in the evolution of 2575 cobs found in five successive strata in Cebollita Cave in New Mexico.

2. The evolutionary sequence starts at Level 5 with a pure type of Chapalote, the indigenous race from this part of North America. Identification of this original Cebollita maize as Chapalote was possible because its morphological details were perfectly preserved by carbonization.

3. After a period of abandonment of the cave most of the maize in Level 4 changed abruptly to a highly Tripsacoid type of Chapalote which was becoming prevalent in the Southwest. Some of the more Tripsacoid of these specimens resembled, in induration and appearance, segregates from experimental hybrids between maize and teosinte, while other specimens remained identical to the original pure type.

4. The immediate effect of the teosinte introgression was to cause a marked reduction in average cob-size to the lowest values of the site.

5. Although advances to higher Levels (3, 2, 1) were marked by a progressive decrease in the indurative effects of this introgression, the variability in cob size which was introduced by the introgression continued to increase. For cob diameter, increases in variation cease at Level

3. But for cob length, the expanding variation proceeds up one level higher.

6. The same type of parabolic relationship between teosinte introgression and cob-length which was found in a previous study of cobs from Richards Cave in Arizona was also found in the Cebollita Cave cobs. The interpretation of this type of relationship is that the long Tripsacoid cobs are the vigorous products of heterozygous teosinte germplasm, while their short counterparts show the detrimental effects of homozygous teosinte germplasm.

7. In the final evolutionary products from Levels 2 and 1 at Cebollita, there is almost complete recovery from the detrimental effects of teosinte introgression and many of the cobs are larger and probably more productive than the original Chapalote maize. Some of these superior cobs resemble those of the present day maize from the Southwest.

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During the course of the investigation and preparation of the manuscript, many helpful suggestions were made by Professor Paul C. Mangelsdorf of Harvard University.

TABLE I. A comparison of the ear characteristics of archaeological maize from Cebollita and Cottonwood Caves to that of modern Chapalote from Mexico.

	Cebollita	Cottonwood[1]	Chapalote[2]
External Characters of Ear			
Length (cm.)	8.7	9.0	11.0
Diameter (cm.)	2.6	3.3	2.9
Row Number	10.5	14.0	12.3
Width of Kernel (mm.)	6.0	6.0	6.7
Thickness of Kernel (mm.)	4.0	4.0	4.1
Length of Kernel (mm.)	7.1	—	7.4
Internal Characters of Ear			
Diameter of Cob (mm.)	19.0	—	22.0
Diameter of Rachis (mm.)	12.0	—	11.2
Length of Rachilla (mm.)	2.0	—	1.8
Glumes	prominent	prominent	prominent
Cupule Wings	prominent	—	prominent
Teosinte Introgression	1	—	—

[1] Data from Hurst and Anderson (1949).
[2] Data from Wellhausen *et al.* (1952).

TABLE II. Morphological characteristics of five strata of archaeological maize cobs.

		Level 5	Level 4	Level 3	Level 2	Level 1
Total population		200	613	798	903	61
Carbonized	%	85	44	0	0	0
Charred	%	15	1	0	0	0
Intact	%	7	10	27	23	33
Fasciated	%	27	18	20	21	23
Unusual	%	3	5	3	4	4
Teosinte Introgression (%)	1 (low)	100	15	18	20	25
	2	—	37	38	48	50
	3	—	30	22	24	12
	4	—	15	19	7	5
	5 (high)	—	3	3	1	1
No. of Kernel Rows (%)	4	—	3	2	1	2
	6	—	—	1	1	—
	8	27	48	39	39	38
	10	32	30	35	35	41
	12	33	16	20	21	16
	14	5	2	2	3	3
	16	3	—	—	—	—
Diameter mm. (%)	10	—	—	1	—	—
	12	—	3	4	2	—
	14	—	14	11	11	11
	16	10	24	24	20	35
	18	40	39	31	30	32
	20	48	18	23	29	16
	22	5	2	5	6	6
	24	—	—	1	1	—
	26	—	—	—	1	—
Length cm. (%)	3	—	—	3	2	—
	4	—	8	7	10	5
	5	—	29	15	17	15
	6	—	19	22	17	20
	7	11	20	17	14	20
	8	34	9	13	14	15
	9	25	7	8	9	10
	10	30	4	6	8	10
	11	—	—	4	5	—
	12	—	4	3	4	—
	13	—	—	1	—	—
	14	—	—	1	—	5
	15	—	—	—	1	—

— Absent

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